Technical Bulletin No. 80 May, 1927

1927

IMPERIAL BUREAU
16 JAN 1929
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VIRUS DISEASES OF RASPBERRIES

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ACKNOWLEDGEMENTS

The writer is much indebted to Dr. G. W. Keitt and to Professor L. R. Jones of the University of Wisconsin for many helpful suggestions and criticisms, and to Dr. E. A. Bessey and Dr. G. H. Coons of Michigan State College for advice during the course of the work.

The insects used in the transmission experiments have been identified by Miss Eugenia McDaniels of the Department of Entomology, Michigan State College, to whom the writer wishes to express his gratitude for help and advice on the insect phases of the problem.

Professor R. E. Loree of the Horticultural Department, Michigan State College, has very kindly furnished many of the plants used in the inoculation work and varietal studies.

VIRUS DISEASES OF RASPBERRIES

By C. W. BENNETT

Growers of small fruits over the United States and Canada have recognized for many years that continuous and intensive culture of raspberries has resulted in a falling off in yield of fruit and to the production of smaller and less thrifty plants in nearly every section in which the industry has become well established. As a result, raspberry growing has been practically discontinued in many of the older sections and, in many others, the industry is on the decline. Many things, such as soil depletion and running out of varieties, have been suggested as causes for this condition, and a considerable part of the loss involved has been attributed to what has been called "raspberry yellows." There has been much confusion regarding the name "yellows" and the symptoms which this term has been supposed to embrace.

At the suggestion of Dr. G. W. Keitt, investigations were started during the summer of 1922 to determine the nature, methods of spread, and control of "yellows" and the relation which "yellows" has to the decline of the raspberry industry in certain localities and to the failure of certain promising varieties to continue production of vigorous plants and high quality fruit. These investigations have continued through four seasons, part of the work being done at the University of Wisconsin and the remainder at Michigan State College. It has developed through these studies and through work done by investigators who will be mentioned later, that the old term "yellows" has probably been used to include a number of separate and distinct sets of symptoms or distinct diseases of the virus type. The following report deals mainly with virus diseases of the red, black, and hybrid varieties of raspberry. However, it is known that other species of *Rubus*, the blackberry and dewberry in particular, are in some cases attacked by the same or similar diseases. The diseases of blackberry and dewberry have as yet not been sufficiently investigated to permit a report at this time.

History

Virus diseases of raspberry probably caused widespread loss in the fields of small fruit sections long before these troubles were recognized as distinct diseases. The raspberry is attacked by numerous diseases of a fungus or bacterial nature and is preyed on by many insect pests. It is a plant which also declines rapidly in productiveness and vigor under adverse soil and cultural conditions. These various factors singly and in combination have no doubt been used to explain low yields and poor quality of fruit in many instances in which virus diseases, which are now known to be widely distributed, were

responsible. It was not until about 1895 that the virus diseases of cane fruits began to be distinguished as troubles distinct from diseases caused by bacteria, fungi, and poor nutritional conditions; and it was several years after this date that something approaching a conception of the true nature of these troubles was obtained.

Detmers (12) probably first described virus disease symptoms on raspberry; and, judging from the description, one of the diseases with which she was dealing was probably mosaic, although the damage done to affected plants was at the time attributed to bacteria.

Green (14, 15) mentioned "leaf curl" in a report of the Minnesota station for 1894 and the next year stated that "During the last five years the disease known as 'leaf curl' has seriously affected almost every variety of red raspberry on the grounds of the University Farm. Almost nothing as yet is known of the history of the disease although its ravages are widespread over the country."

Reports of disease came from other sections of the country and, in 1902, Stewart and Eustace (30) published a study of cane blight in connection with a trouble for which they chose the name "yellows." This name was chosen, as the authors state, because it described the condition of affected plants and not because of any supposed relation to peach yellows. Yellowing of the foliage of several red varieties of raspberries when infected by mosaic is quite characteristic and it is quite probable that mosaic was the predominating virus trouble in the plantings which Stewart and Eustace described.

In 1924, Melchers (21) described curl in Ohio and suggested that the name "curl", as used by Green, was much more descriptive of the appearance of diseased plants than was the term "yellows." Melchers was undoubtedly dealing mainly with the disease which is now known as curl, though a part of his description and the varieties named as affected would indicate that perhaps "yellows" symptoms as described by Stewart and Eustace were also present.

Dickson (9), in 1920, presented an abstract in which he states, "Raspberry mosaic is clearly differentiated from yellows," and in a later publication (10) he makes the term "curl" synonymous with "yellows", though he suggests that it would be more fitting to make "yellows" synonymous with mosaic. Rankin and Hockey (26) suggested that two diseases were included under the term "yellows" and proposed that they be called mosaic and curl. The same year, Wilcox (31) published a report on a disease of black raspberries, characterized by symptoms very different from those associated with diseases of this type which had been described previously. This disease on affected plants produces certain characteristic stem markings and for this reason was first called "eastern blue stem." Rankin (24), because of certain foliage characteristics, later called the same disease "rosette." Zeller (34) has since changed the name to "streak," which seems to be a very appropriate name and one which merits general use.

Curl and mosaic have been recognized as distinct diseases in studies of virus troubles in Michigan fields of red raspberries since 1922. In the course of these investigations what appears to be two additional mosaics, both on black raspberries, have been identified and transmitted. One of these, because of its characteristic effects on the plant, has been called "mild mosaic." This disease is quite common on all black

varieties which have been investigated and seems likely to become an increasingly important factor in commercial raspberry growing. The second disease, called "yellow mosaic" because of the yellow cast of the foliage of infected plants, is well distributed but not seriously destructive.

These five diseases; namely, curl, red raspberry mosaic, mild mosaic, yellow mosaic, and streak, account for most of the so-called "degeneration" of raspberries under Michigan conditions; and this is probably true also for other parts of the United States and Canada.

Economic Importance and Distribution

Virus diseases as a group are by far the most destructive of all of the raspberry troubles. The immediate loss to the grower is often large, but perhaps the most important influence of these diseases has been exerted on the small fruit industry as a whole. These diseases have caused the loss of the best quality in fruit in valuable varieties, and have caused low yields, and general discouragement on the part of the growers.

These losses have undoubtedly occurred since the early history of raspberry growing in the United States, but in recent years they have seemed to become more widespread and severe. Green (14) in 1895 reported that leaf curl was much more important in Minnesota than was anthracnose and was seriously affecting all of the red varieties grown. Reports from the northeastern states indicate, in the light of our present knowledge, that virus diseases have long been an important factor in the decrease of acreage devoted to raspberries and related crops in many of the older small fruit sections; and that the diseases have also been the chief causes for the discarding of many popular varieties. Stewart and Eustace (30) reported in 1902 that the Marlboro variety was being abandoned in the Hudson River Valley, and this once much grown berry has since largely disappeared from commercial plantings. The Perfection and Empire have likewise become so generally diseased that they have ceased to be of commercial value and the Cuthbert variety, according to Rankin (24), is even now being abandoned in New York State because of mosaic and curl. Melchers (21), in 1914, reported that curl in Ohio was causing losses estimated by growers at $200 an acre. This disease, it is said, was probably the chief factor in an eighty per cent reduction in acreage devoted to raspberries in Lucas and Cuyahoga counties in a period of eight years. Both, red raspberry mosaic and curl are prevalent in Canada. Hockey (17), in 1921, estimated that from twenty to thirty per cent of the Cuthberts were infected by mosaic in a number of townships and that Marlboro was even more diseased. Virus diseases are quite prevalent in bramble fruits on the Pacific Coast, according to Zeller (34), and are causing considerable loss. Reports from Illinois, by Colby and Anderson (6), indicate that, in many sections, raspberries are severely affected by virus diseases. Streak is estimated by Wilcox (31) to be causing an annual loss of $10,000 in the Dover Avon districts of Ohio. Virus diseases have been reported from the British Isles by Grubb and Massee (16). Apparently, these diseases are common on raspberries in the plantings which they have examined and are of considerable economic importance.

From the foregoing brief summary of reports, it is evident that virus diseases in raspberry are widely distributed; and it is probable that two of these, red raspberry mosaic and curl, are present in every raspberry section in the United States and Canada. It is also probable that a rather high percentage of the plants of all red varieties is infected by mosaic. Mild mosaic as a disease of black varieties is probably almost as common as red raspberry mosaic on red varieties, although in this case distribution records are not complete. In Michigan, mild and red raspberry mosaic are by far the most common of the virus diseases.

The King variety in Berrien County is badly infested by mosaic, though in other parts of the state this variety is relatively clean. The Cuthbert in general in this state has shown very little mosaic, though considerable curl is frequently observed in plantings of this variety. In rare cases, fields show seventy per cent curl, but usually less than ten per cent of the plants of individual fields are affected by this disease. Many blackcap fields of Cumberland and Plum Farmer show from five to thirty per cent of the plants to be affected by mild mosaic.

This disease is widely distributed and is found in the majority of the plantings in the state. In general, it has not been so destructive from the standpoint of berry production as have some of the other troubles. Affected plants decline slowly, and yield fair crops of fruit for a considerable time after becoming infected.

Yellow mosaic in Michigan, although it is widely distributed over the state, has never been found to affect more than two per cent of the plants in any commercial planting. It is probable that this disease causes very little loss. Its distribution outside of Michigan is not accurately known, though it has been observed in Wisconsin, Minnesota, New York, and Ohio.

Streaks seems to be most prevalent in Ohio and Illinois; Wilcox (31) reports a high percentage of this disease in plantings in the vicinity of Cleveland, and Colby and Anderson (6) have found the disease quite common in northern Illinois and well distributed in the raspberry fields of the state. Streak is also to be found to a limited extent in Wisconsin, Michigan, and New York, and probably elsewhere. It has been found in Michigan in only a few locations and in only one commercial planting. In this streak-infested field, about ten per cent of the plants showed the disease in various stages of development.

Description of Symptoms

The virus diseases of raspberry may be readily separated on the basis of symptoms and are easily recognized under field conditions. On what may be called standard varieties of raspberries, the symptoms of each individual disease seem to be rather distinct and, under ordinary weather conditions, reasonably constant. These diseases, however, differ from each other quite markedly and if the group is considered as a whole there is probably as wide a range of virus disease symptoms, such as leaf curling, mottling, yellowing, stem streaking, and necrosis, as is to be found in the groups of virus diseases of such plants as tobacco and tomato. While the field symptoms of the different diseases are sufficiently distinct for purposes of diagnosis,

use of these is by no means the only way of distinguishing one disease from another. Other peculiarities such as varietal susceptibility and resistance, temperature relations, and disseminating insects are frequently important aids in differentiating these diseases.

The following classification and description of these troubles is presented with the aim of furnishing a basis for further work, and in no sense should be considered complete. While the five types of virus troubles described represent a classification which seems to include all of the "degeneration" troubles in Michigan, it is by no means certain that other types equally distinct may not be present in other parts of the United States or even in this state. It is also entirely possible that closer study may reveal that two or more separate sets of symptoms have been included under one description. It has been suspected that in the case of mosaic of red raspberries there may be more than one virus involved. However, differences which have been observed in diseased plants, which would lead to this conclusion, are largely differences in degrees of mottling and stunting and as yet no special attempt has been made to obtain finer separation.

Curl. This disease is found on red, hybrid, and black raspberries and also on blackberry. Although cross inoculations have not been successful in all cases, the symptoms are so similar on susceptible varieties of these different groups, that it is assumed for the present that there is only one disease involved.

The Cuthbert, among the red varieties, and the Haymaker and Cumberland, of the purples and blacks, are very susceptible to curl. On these varieties, the characteristic symptoms consist of a curling of the leaves accompanied by the production of a deep green foliage and by a stunting of the entire plant. The curling of the leaves seems to be due to retardation in growth rate of the veins while the intervening tissue continues to grow at a more or less normal rate, resulting in the apparent sinking of the veins, a downward curling of the leaf margins, and the production of folds or crinkles in the other parts. The leaves and canes of curl plants appear dry and do not wilt so readily as normal plants. By late summer, the leaves have usually taken on a bronze color, thus giving the entire plant a coloration which in some instances is quite in contrast to the lighter green foliage of the surrounding healthy individuals. The degree of leaf rolling varies somewhat with the character of the soil on which the plants are growing and with the rate of growth. Slow-growing plants usually show very distinct curl symptoms. On plants growing more rapidly, symptoms are likely to be somewhat less marked. In some cases of Cuthbert plants growing on very fertile soil, it has been difficult to distinguish curl plants from healthy ones. In such cases, there may be practically no curling of the leaves and at first very little stunting of the canes. Diseased leaves may be only slightly roughhened in appearance and just a shade deeper green than normal. However, in all cases, there is a characteristic greasy appearance of the leaf surface. Usually under field conditions, curl symptoms are quite marked and there should rarely be any doubt as to the presence or absence of this disease.

Curl symptoms, resulting from the current season's infection, often appear on the tips of the new canes by the first of July. The symptoms

are usually characteristic and marked, even in the very early stages. In the season which follows infection, all parts of the plant show curl. The new canes will be considerably stunted and become more so each succeeding season. Canes occasionally have a tendency to branch excessively, sometimes profusely, and in proportion to wood produced, have a rather large pith.

Diseased canes lack hardiness and are very subject to winter killing. Fruiting canes produce very short fruiting shoots even the first season after infection. This is especially true of the Haymaker which ordinarily produces a fruiting shoot 18-20 inches long, but when attacked by curl may produce shoots 6-8 inches long with berries placed close together. This reduction in length of fruiting parts accompanied by reduction in leaf surface gives the appearance of a stocky plant loaded with berries, and had led to the conviction on the part of some growers that curl plants produce a greater number of fruits than do healthy ones.

Berries on diseased plants are small and of poor quality. Weighings made from healthy Cuthbert plants and from plants which had been diseased less than a year indicated that curl plants produce berries which are from twenty to forty per cent lighter than those from normal plants. This reduction is still greater in the case of some of the purple and black varieties. Such fruits are insipid, and the quality and size of fruit continue to decrease the longer the plants have the disease. Berries on curl plants are usually so small and of such poor quality that they are rarely harvested.

Curl plants may live for a number of years. Cuthberts are said to have lived eight years and frequently live five or six years after contracting this disease. Haymaker plants usually die the third or fourth season and Cumberland plants frequently succumb in even a shorter time.

Red Raspberry Mosaic. This disease is found on red, purple, and black varieties of raspberry and perhaps on blackberry and dewberry. The name is chosen because this seems to be by far the most common and destructive virus disease on red raspberry. Although the same disease is known on black varieties of raspberry and there is a probability that it also occurs on other bramble fruits, it is not believed to be of any considerable economic importance on any of these forms.

This disease varies greatly in its effect on different kinds of raspberries. Some varieties produce typical mosaic mottling characterized by distinctly yellow distorted leaves with dark green elevated blisters. Still other varieties produce leaves which are normal in appearance except for a few yellow blotches. The Cuthbert usually produces distinct mottling but several variations have been observed. Some plants have produced leaves which, when young and up until they were almost full grown, appeared healthy except for poorly defined darker regions about half of a centimeter wide along the main veins. As the leaves become older, the darker areas become more distinct by taking on a deeper green color while the intervening tissue fades to various shades of yellow or yellowish green. Plants with this type of leaf show very little stunting and seem to be capable of thriving for a considerable time in spite of disease. Plants showing more decided

mottling are usually considerably stunted after the second or third year.

Such forms as St. Regis and Sunbeam show very little mottling and this only as a result of low temperature. Some wild plants of the species *Rubus strigosus* carry virus through an entire season and show no symptoms of mottling, except on the very first leaves produced in the spring and on the late growth of the fall. Other plants of this species show quite distinct symptoms throughout the growing season.

Some other varieties do not show any symptoms which are strictly characteristic of the disease on Cuthbert. The Empire and Perfection varieties are thoroughly infested and perhaps have been so for an indefinite period, yet plants of these varieties produce a fair yield and make an average vegetative growth. In general, the leaf symptoms consist of yellowish blotches of varying shades, sometimes very distinct but often obscure and confusing. However, at times dark green elevations may be found on the leaves of affected plants. The Latham and the King varieties, in their reaction vary from very faint indications of mottling to a quite distinct blistered condition, though the latter symptom is less common.

Purple raspberries react to red raspberry mosaic in much the same way as do red varieties. On the Columbian, two rather distinct types of mottling may be observed. In one case, the mottling is very mild and appears only on those leaves which are developed at a low temperature. No appreciable dwarfing has been associated with this type of disease. On other plants very characteristic mottling, yellowing, and dwarfing occur. On Haymaker and Royal Purple, symptoms are masked during the greater part of the season. Definite mosaic symptoms have never been found on the Cardinal variety. This raspberry apparently is either very resistant to infection or masks symptoms almost completely under average growing conditions.

The influence of red raspberry mosaic on the yield of fruit varies much with the different varieties. On a severely affected variety such as Cuthbert, the yield is usually reduced to a considerable extent in a relatively short period. The quality of fruit is also considerably impaired. A variety such as St. Regis will probably bear nearly a normal crop for a considerable time, even though every plant in a field be infected. However, raspberries which at first show least injury are probably most likely to be discarded as "run out" varieties.

Red raspberry mosaic may be found also on black varieties. In strong contrast to its effect on red and purple forms, this disease on black caps is quickly destructive to the affected plant. The first indication of infection is found usually in the stunting of the tip of one of the first year canes. Such tips often curve and frequently a brown or very dark stripe is produced on the concave side. The leaves on this side turn yellow and usually die. The following year a plant is obtained which has fruiting canes of normal size, but with short fruiting shoots which produce "seedy" berries of poor flavor. The new canes which are produced the season following infection usually reach a height of not more than two feet. These stunted canes have short internodes and the leaves are consequently thrown close together, presenting a rosetted condition. The tips of the growing shoots soon

become discolored and towards the end of the season in most cases die. A short distance below the terminal bud, reddish to brownish splotches appear on the cane. These may be merely small spots or may be discolored areas an inch or more long and which reach half way around the cane (Pl. III, Fig. 3). Leaf petioles usually show the same type of markings although the discolorations often take the form of narrow fringed lines which pass half way around the petioles. Leaf petioles and cane tips are very brittle. The pith of the canes is discolored as are certain parenchymatous cells of the bark and of the leaf petioles. The discolored areas, which can be seen from the surface, are caused by groups of cells which appear to be filled by a substance of a gummy nature.

Sometimes the terminal bud on stunted shoots resumes growth, but more often new shoots are put out from lateral buds lower down on the cane. For a time laterals thus formed may make a rapid and vigorous growth. If the temperature is high these new shoots may show no symptoms of mosaic until they have grown to considerable length. Mottling may or may not be evident. Such mottling as does appear exhibits considerable variation. In some cases, the leaves are yellow and dwarfed on one side, other leaves show a fine grained pattern of mottling consisting of small yellow spots surrounded by tissue of deeper green color. The majority of leaves, however, show little or no mottling. Leaves in general are deeper green than are leaves of healthy plants, and those which are produced on the fruiting canes often have the leaflets slightly rolled at the edges.

Mild Mosaic. For several years a mild form of mottling has been observed on a number of different varieties of black raspberries. This mottling is most evident on the leaves of the fruiting canes and on the lower leaves of the first year canes. Leaves may show only a trace of discoloration or a faint pattern of mottling or the mottling may take the form of distinct, raised, darker green areas surrounded by a field of yellow. Extreme symptoms such as those shown on the leaf in Plate IV, Figure 1, appear at low temperatures. As the temperature increases, symptoms become less marked until at average summer heat mottling is completely masked. Leaves of young canes at times produce yellowish and rather inconspicuous spots along the veins and in the angles of the veins (Plate IV, Fig. 3.). Such spots characteristically appear when plants are grown at a temperature slightly below the maximum for symptom expression.

Plants grown in the greenhouse at a low temperature often produce distorted leaves, and frequently the lighter colored leaf tissue dies in spots, producing a condition very similar in appearance to the Septoria leaf spot of raspberry. Very little of this type of injury, however, has been noted in the field. Mild mosaic plants examined in the late summer or fall after the fruiting canes have died or have been removed generally show symptoms only on occasional leaves or rings of leaves on the new canes.

Under some conditions, the leaves of these rings are of normal size and do not differ from the other leaves on the same cane except in their mottled appearance. In other cases, the mottled leaves are decidedly dwarfed, and, in some instances, the leaves are partly or wholly killed. Figures 4 and 5 of Plate IV show dwarfing of leaves. Some

of the leaves shown in Figure 5 were nearly dead when the canes were photographed. Rings of mottled and dwarfed leaves mark periods of relatively low temperatures.

The rate of decline of plants affected by mild mosaic has not been accurately determined. It is known that diseased plants produce well for a considerable time and that the first and second crops of fruit produced are sometimes not materially decreased either in quantity or quality. Mild mosaic plants of the Munger variety have been under observation for four years. These plants were all diseased when they were started as tips in 1922 but the time of infection is unknown. The plants produced a fair growth the first season in which they fruited but have since lacked vigor and productiveness. Canes have been weak and tips have rooted poorly. Tips from these plants grown in the greenhouse have uniformly produced spindling shoots, which have in many cases died before they reached any considerable size.

Yellow Mosaic. Generally distributed over the state and appearing on all of the leading varieties of black raspberries, is still another type of disease which is different in many of its characteristics from the other virus diseases of Rubus which have been described. Affected plants are short lived and are usually killed the second or third winter after infection. During the summer, infection takes place on the tips of the growing shoots. Such shoots soon begin to produce a mottled condition varying from very faint splotches to distinct yellowish patches. There is usually, however, not much evidence of raised areas such as are usually found on some varieties affected by red raspberry mosaic.

The season following infection the entire plant shows marked symptoms of disease. Fruiting canes produce fruiting shoots which are short and weak, and these develop berries which have a tendency to be "seedy" and crumbly. New canes are usually weak and inclined in some cases to grow nearly parallel to the ground instead of upright. Leaves are often flat; but at times the leaflets are turned down at the edges, presenting a spoon-shaped appearance.

Plants will tip the first and second seasons following infection, and diseased tips undoubtedly aid in spreading this trouble. However, the third year a very feeble growth is produced and, if the plant survives the summer, it rarely lives through the following winter.

Streak. Black raspberry varieties in general are susceptible to streak. Wilcox (31) has reported this disease on black varieties in Ohio and also what appears to be the same or a similar trouble on blackberry. As yet no cases of the occurrence of this disease on red varieties of raspberry have been observed.

Diseased plants present an appearance which suggests mild leaf curl symptoms. Plants are stunted after the first year and become smaller each succeeding season. Leaves on such plants are nearly always distinctly curled and usually placed close together on the canes. The foliage is a shade darker green than normal. Leaves, especially those at the tip of the canes, have a peculiar twist of the midrib, with a decided tendency to bend at an angle and recurve in such a way as to bring uppermost the dorsal side of the tips of the leaflets.

As this disease has been observed under Michigan conditions, mottling has not been a constant character; and the mottling which has been

fection may at times occur on plants considerably removed from a source of inoculum. In 1923, twenty-two separate infections were produced in a planting of Cuthberts on the Experiment Station grounds when the closest curl plant was nearly two hundred yards away and there were only three plants in this location. In 1924, evidence was obtained that curl spread to two plants in a lot of one hundred and twenty, from a distance of approximately a half mile.

Frequently, mild mosaic on black varieties and red raspberry mosaic on red varieties seem to spread at a very rapid rate. Red raspberry mosaic on black varieties spreads very slowly, as a usual thing, due evidently to the short life of infected plants. Yellow mosaic also spreads slowly and it is probable that this disease will not become of great economic importance. Streak has spread very slowly under Michigan conditions. Reports from other parts of the United States, however, indicate that this disease may spread very rapidly, and, in the course of two or three seasons it may attack a considerable percentage of the plants in a field.

Disseminating Agents

Under Michigan conditions, there are three species of aphids common on red, purple, and black raspberries. These are *Aphis rubiphila* Patch, a rather small aphid; *Amphorophora rubi* Kalt, a large aphid which feeds chiefly on the leaves; and *Amphorophora sensoriata* Mason, another insect of considerable size which is found in abundance on the stems of black raspberry and in smaller numbers on the stems of purple and red forms. There are, of course, numerous other sucking insects which offer possibilities in investigations on spread of disease of the virus type, but most work has been done on the three species of aphids named. Two of these have been shown by different investigators to be factors in the spread of virus diseases; the third, *A. sensoriata,* has not as yet been connected with the dissemination of any known virus disease, although numerous tests have been made.

Rankin and Hockey (26) transferred curl from diseased to healthy Cuthbert raspberries by means of *Aphis rubiphila,* and Dickson (10), in 1922, reported transfer of mosaic (presumably red raspberry mosaic) in three instances by an aphid which he assumed to be *A. rubiphila.* Wilcox and Smith (33) later showed that red raspberry mosaic could be transmitted to blackcaps by *Amphorophora rubi.* In publications on virus diseases of raspberry, however, this insect has been given very little consideration as a disseminating agent, *A. rubiphila* in nearly all cases having been considered as the chief insect involved, although complete evidence to this effect has been lacking.

Experimental Work in Transmission of Virus Diseases by Insects

The inoculation experiments reported in this paper have been carried on over a period of more than four years. During the first three seasons, *Aphis rubiphila* was used almost exclusively because of the ease of keeping stock supplies of this insect. In the earlier work, *Amphorophora rubi* was used only in a limited number of experiments, but, during 1924 and 1925, this aphid was employed in an extensive series of inoculations. *Amphorophora sensoriata* Mason was tried in

Table 1.—Summary of Results of Representative Experiments in the Transmission of Virus Diseases of Bramble Fruits.

Varietal source of inoculum	Aphid used in transmission	Disease involved	Variety inoculated	No. of plants inoculated	No. of plants diseased
Cuthbert (R)	Amphorophora rubi	R. R. Mosaic	Cuthbert (R)	10	3
Cuthbert (R)	Amphorophora rubi	R. R. Mosaic	King (R)	10	6
Cuthbert (R)	Amphorophora rubi	R. R. Mosaic	Gregg (B)	10	10
Cuthbert (R)	Amphorophora rubi	R. R. Mosaic	Cumberland (B)	10	9
Cuthbert (R)	Amphorophora rubi	R. R. Mosaic	Plum Farmer (B)	10	10
Cuthbert (R)	Amphorophora rubi	R. R. Mosaic	Columbian (H)	10	4
Cuthbert (R)	Aphis rubiphila	Curl	Cuthbert (R)	10	10
Cuthbert (R)	Aphis rubiphila	Curl	Haymaker (H)	10	7
Cuthbert (R)	Aphis rubiphila	Curl	Viking (R)	10	2
Cuthbert (R)	Aphis rubiphila	Curl	Wild Red (R)	10	3
Cuthbert (R)	Aphis rubiphila	Curl	Lucretia Blackberry	10	4
King (R)	Amphorophora rubi	R. R. Mosaic	King (R)	10	7
King (R)	Amphorophora rubi	R. R. Mosaic	Cuthbert (R)	10	2
Perfection (R)	Amphorophora rubi	R. R. Mosaic	Gregg (B)	10	9
Perfection (R)	Amphorophora rubi	R. R. Mosaic	Plum Farmer (B)	10	7
St. Regis (R)	Amphorophora rubi	R. R. Mosaic	Gregg (B)	10	7
Wild Red (R)	Amphorophora rubi	R. R. Mosaic	Plum Farmer (B)	10	8
Wild Red (R)	Aphis rubiphila	Curl	Wild Red (R)	10	7
Wild Red (R)	Aphis rubiphila	Curl	Cuthbert (R)	10	4
Haymaker (H)	Amphorophora rubi	R. R. Mosaic	Haymaker (H)	10	2
Haymaker (H)	Amphorophora rubi	R. R. Mosaic	Cuthbert (R)	10	1
Haymaker (H)	Amphorophora rubi	R. R. Mosaic	Gregg (B)	10	10
Haymaker (H)	Amphorophora rubi	R. R. Mosaic	Columbian (H)	10	7
Haymaker (H)	Aphis rubiphila	R. R. Mosaic	Cumberland (B)	10	1
Haymaker (H)	Aphis rubiphila	Curl	Haymaker (H)	10	5
Haymaker (H)	Aphis rubiphila	Curl	Cuthbert (R)	10	7
Columbian (H)	Amphorophora rubi	R. R. Mosaic	Columbian (H)	10	6
Cumberland (B)	Amphorophora rubi	M. Mosaic	Cumberland (B)	10	10
Cumberland (B)	Amphorophora rubi	M. Mosaic	Gregg (B)	10	10
Cumberland (B)	Amphorophora rubi	R. R. Mosaic	Cumberland (B)	10	3
Cumberland (B)	Amphorophora rubi	Y. Mosaic	Plum Farmer (B)	10	10
Cumberland (B)	Aphis rubiphila	Curl	Cumberland (B)	10	7
Cumberland (B)	Aphis rubiphila	Curl	Cuthbert (R)	10	8
Gregg (B)	Amphorophora rubi	M. Mosaic	Gregg (B)	10	8
Gregg (B)	Amphorophora rubi	Y. Mosaic	Gregg (B)	10	10
Gregg (B)	Amphorophora rubi	Y. Mosaic	Plum Farmer (B)	10	9
Plum Farmer (B)	Amphorophora rubi	M. Mosaic	Plum Farmer (B)	10	7
Plum Farmer (B)	Amphorophora rubi	Y. Mosaic	Plum Farmer (B)	10	3

R—Red raspberry. H—Hybrid or purple raspberry. B—Black raspberry.

several series of inoculations made during 1926 and was earlier used to a limited extent in 1925.

To a large extent, potted plants have been used for these transmission tests but many plants growing under field conditions have been inoculated. Before inoculation, plants were grown in cold frames where they could be watered regularly and kept in a thrifty, rapidly growing condition. Inoculated plants have been placed in cheesecloth cages along with suitable checks, or in greenhouses where aphids could be controlled.

Table 1 shows the results of experiments selected from those which have been performed during the course of these investigations. Only a small percentage of the results of inoculation experiment actually performed is shown but these results are from representative tests. All experiments have been repeated at least once, and many of them have been performed several times.

Curl has been transmitted repeatedly on susceptible varieties since 1922. This disease is readily transmitted and infection is obtained in a high percentage of plants inoculated if *Aphis rubiphila* is used as the insect carrier. Infected plants begin to show symptoms in from sixteen to thirty-five days after inoculation. The first indication of disease

ferent symptoms is the same on black varieties. The Gregg has been chosen as the standard variety for these tests. It has been found by these experiments that virus transferred from a distinctly mosaic Cuthbert gives exactly the same initial reaction on the black variety as does virus from a St. Regis or a wild red raspberry plant in which symptoms of mosaic are barely visible. Other red varieties and plants of the Cuthbert variety showing different degrees of mottling have been used; but, on Gregg, symptoms in the early stages of disease have been practically the same in all instances. Infected plants, however, have not been kept for extended observation.

During the season of 1925, this extreme susceptibility of black varieties to red raspberry mosaic and the short incubation period were used to a considerable extent in diagnosing mosaic on red varieties in which symptoms are obscure. This method has also been found useful in determining infection on inoculated plants of red varieties in which symptoms are partially or wholly masked during the summer. In two series of ten plants each, wild red raspberry plants were inoculated with mosaic and, three weeks after inoculation, the plants were fumigated. Ahpids which were free from the mosaic virus were then placed on these plants and after being allowed to feed for six days were transferred to healthy Gregg plants; four Gregg plants being inoculated from each original plant. By this means, it was found that three wild red raspberry plants in one series and five in the other series were infected by mosaic virus, though no symptoms were evident on the plants themselves.

It is believed that blackcap tests similar to the above will prove of value to investigators in testing out original stock of red raspberries, or for making tests for mosaic virus in any red variety in which absolutely healthy plants are especially desired.

Mild mosaic is another disease which is readily transmitted by *Amphorophora rubi*. July 16, 1924, three series of ten plants each were inoculated with mild mosaic by means of this aphid. Thirty days after inoculation nineteen of these plants showed symptoms of mottling. The plants were allowed to remain in the cages in the presence of aphids for an additional period and were started in the greenhouse the following February. Each series showed one hundred per cent infection. Gregg and Plum Farmer were the varieties used for inoculations. Of an equal number of plants inoculated with mild mosaic by means of *Aphis rubiphila* and later subjected to the same treatment, all have remained healthy. These experiments were repeated in 1925 and 1926 with essentially the same results as those obtained in 1924. *Amphorophora sensoriata* has been used in several series of trials but inoculated plants have shown no evidence of infection.

The incubation period of mild mosaic has varied from eighteen to thirty days. First symptoms appear on the young leaves and have been most marked on leaves about two-thirds grown. The mottling is something distinct but more often of a milder type similar to that shown on the leaf in Plate IV, Figure 3, and consists of small pale yellowish splotches located chiefly in the angles and along the edges of the veins.

Yellow mosaic has been transmitted in two cage experiments and in several single plant inoculations in the field by means of *Amphoro-*

phora rubi. In July 1925, each of twenty plants of the Gregg and Plum Farmer varieties were inoculated with ten aphids taken from a Cumberland plant affected by yellow mosaic. Sixteen of these plants showed symptoms of mosaic during the season of 1925 and all plants have shown very decided yellowing, mottling, and dwarfing after being grown the second season in the greenhouse. Transfers of aphids made to the red varieties Cuthbert and King have been followed by no signs of infection. Numerous attempts have been made to transmit yellow mosaic by means of *Aphis rubiphila,* and thirty plants have been inoculated by means of *Amphorophora sensoriata* but neither of these aphids have transmitted the disease in these tests.

First symptoms of yellow mosaic appear on the young leaves. A slight yellowing accompanied by a limited amount of mottling is noticeable on the very young leaves eighteen to thirty days after inoculation. These symptoms become more pronounced as the leaves enlarge, and subsequent growth has the characteristics already described. Very little necrosis has been associated with infected plants during the season of infection. These plants grown in the greenhouse the following spring, however, do show a tendency to produce dead areas on the leaves and at the growing tips. The younger leaves often twist and turn a dark brownish color. Leaves taken from these plants and placed in moist chambers darken in less than two hours under conditions which maintain healthy leaves and mild mosaic leaves in approximately normal condition for three days.

Plants showing streak were not available for experimental work until late summer of 1925. Several series of inoculations were made during August from tips of canes brought in from Berrien County and kept in tumblers of water. Twenty Cumberland plants were inoculated using *Amphorophora rubi,* ten by means of *Aphis rubiphila,* and twenty by means of *Amphorophora sensoriata.* These plants were started in the greenhouse in February, 1926, but all have remained healthy. These experiments have been repeated during the summer of 1926 without securing evidence of infection.

It will be observed by reference to the above results that there is a decided specificity manifested by the two species of aphids which have been shown to be capable of transmitting virus diseases of raspberries and that one of the most common raspberry aphids, *Amphorophora sensoriata,* has not seemed to be a disseminating agent of any of these virus troubles. In these experiments, *Aphis rubiphila* has readily transmitted curl on all susceptible varieties tried but apparently rarely, if ever, transmits any of the other known virus diseases of this group. *Amphorophora rubi* has transmitted red raspberry mosaic, yellow mosaic, and mild mosaic but does not seem to be an agent of transmission of curl. These insect peculiarities in relation to transmission have been tested still further by a series of inoculation experiments, one of which is reported in Table 2. In this entire series, curl was transmitted only by *Aphis rubiphila,* and transmission of red raspberry mosaic was obtained only with *Amphorophora rubi.* A very low percentage of mosaic infection was obtained on Cuthbert. However, results on Plum Farmer and King seem to constitute evidence sufficient to justify the conclusion that *Amphorophora rubi* is at least the most efficient and probably the chief disseminating agent of red raspberry mosaic. It also

Experiments With Aphids

Plants of the Cuthbert variety affected by curl have been available for experimental work throughout the course of these investigations, and healthy plants have been grown in considerable numbers. Since the Cuthbert variety reproduces by means of suckers, an abundant supply of healthy young plants has been available at all times during the season. Advantage has been taken of this to conduct experiments to throw light on a few points of interest regarding the relation of *Aphis rubiphila* to the curl virus.

Experiments to Determine Whether Curl Virus Overwinters in the Egg of Aphis rubiphila. In the fall of 1922 and again in 1924, potted plants affected by curl and abundantly infested with aphids, were collected in cages. The aphids laid eggs in such numbers that the canes of the plants were almost black. These canes the following spring were cut into short pieces and placed around the base and in the angles of the leaves of young potted plants. Twenty plants were inoculated in each experiment. Aphids hatched from the eggs in considerable numbers and crawled to the growing leaves and stems. It is estimated that, as an average, two hundred and thirty aphids were to be found on each plant. These plants were held from two to three months but no evidence of infection appeared. Check plants inoculated with ten aphids each and held under the same environmental conditions gave seventy per cent infection. Smith (28) has obtained similar results in his experiments with aphid eggs and there seems little probability that the curl virus is carried through the winter in this manner.

Feeding Clean Aphids on Curl Plants for Different Time Periods.

It becomes a matter of considerable importance in inoculation work of this type to know the length of time an aphid must feed on a diseased plant before it becomes capable of acting as an agent of transmission, and suitable for certain types of experimental work.

In August 1923, aphids of the species, *Aphis rubiphila,* obtained from healthy Cuthbert plants were transferred to curl plants. These aphids were later removed to healthy plants at different time intervals, as shown in Table 3. These results indicate that a relatively short time is required to permit aphids to become contaminated with virus; two

Table 3.—Results of Experiment to Determine How Long Aphids of the Species, Aphis rubiphila Must Feed on Plants Affected by Curl Before They Become Capable of Transmitting This Disease to Healthy Plants

Series	Feeding period of aphids on curl plants	No. of plants inoculated	No. of plants healthy	No. of plants diseased
1	Check*	16	16	0
2	2 hrs.	16	10	6
3	4 hrs.	16	9	7
4	8 hrs.	16	5	11
5	24 hrs.	16	11	5
6	48 hrs.	16	9	7

*Aphids from healthy plants.

PLATE I

Fig. 1. Tip of a young red (Cuthbert) raspberry cane showing curl.

Fig. 2. A red raspberry plant affected by curl. This plant was inoculated July, 1924, and photographed August 11, 1925, after the fruiting canes had been removed. All canes show typical curl symptoms.

Fig. 3. A black (Cumberland) raspberry plant affected by curl.

Fig. 4. Curl on a wild red (*Rubus strigosus*) plant. This plant was inoculated from a curl Cuthbert plant by means of *Aphis rubiphila*. Curl symptoms are marked in the younger growth.

Fig. 5. Curl on wild blackberry (*Rubus allegheniensis*). (a) Tip of cane showing first symptoms of disease. (b) Healty tip.

PLATE II

Fig. 1. Red raspberry mosaic showing dark green blisters on a leaf of the Cuthbert variety.

Fig. 2. Red raspberry mosaic on a leaf of the King variety. One-half natural size.

Fig. 3. Mild yellow splotching on a Viking leaf. Two-thirds natural size.

Fig. 4. Yellow blotch sypmtom of red raspberry mosaic on leaves of the variety Perfection. One-half natural size.

Fig. 5. Showing the effect of curl and red raspberry mosaic in dwarfing plants of the Cuthbert variety. (a) Plant infected by red raspberry mosaic in 1923, photographed 1926. (b) Healthy plant. (c) Plant infected by curl in 1923, photographed August, 1926.

PLATE III

Fig. 1. Tip of a Cumberland black raspberry cane fifteen days after being inoculated by red raspberry mosaic. Note the stunted and discolored condition of the terminal growth. One-half natural size.

Fig. 2. A black (Plum Farmer) raspberry plant twelve months after being infected by red raspberry mosaic. Fruiting canes are normal size but few fruiting shoots are produced; the new canes on such plants seldom reach a height of more than eighteen inches.

Fig. 3. Tip of a young black (Cumberland) raspberry cane having red raspberry mosaic. Note the discolored spots on the cane and leaf petioles. Natural size.

Fig. 4. A Cumberland black raspberry plant the season following infection by red raspberry mosaic. The canes in the foreground were produced early in the season; those in the background which are taller, grew during a period of high temperature in late August and early September.

PLATE IV

Fig. 1. Extreme mottling produced on a leaf of Cumberland black raspberry by mild mosaic at a low greenhouse temperature.

Fig. 2. Mottling characteristic of mild mosaic on young canes of black varieties under field conditions.

Fig. 3. Mild mosaic mottling produced just below the maximum temperature limit for the appearance of symptoms.

Fig. 4. A ring of mottled leaves of a young cane of Munger black raspberry. The mottled leaves started expanding during a period of low temperature. None of the other leaves of this cane showed symptoms of mosaic.

Fig. 5. Dwarfing of leaves at low temperatures due to mild mosaic. Note the secondary shoots growing from below the dwarfed area.

PLATE V

Fig. 1. Leaves from a Cumberland raspberry plant which had been inoculated from another black raspberry plant having both yellow and mild mosaic.

Fig. 2. (a) Yellow mosaic leaf and (b) healthy leaf from plants of the Gregg variety of black raspberry.

Fig. 3. A black raspberry plant twelve months after being infected by yellow mosaic.

Fig. 4. (a) Healthy black raspberry cane. (b) Cane from a plant having yellow mosaic. A dark reddish discoloration accompanied by a certain amount of striping suggests streak symptoms.

Fig. 5. A black raspberry plant inoculated by yellow mosaic during the fall of one year and photographed the following July. This plant, except for the yellow leaves, appeared quite normal. The following season, however, the plant was much dwarfed.

PLATE VI

Fig. 1. Tip of a black raspberry cane showing symptoms of streak.

Fig. 2. (a) and (b) Canes from a streak Cumberland plant. (c) Cane from a healthy Cumberland plant. Two-thirds natural size.

Fig. 3. A black raspberry plant of the Cumberland variety showing streak.

Fig. 4. Young greenhouse plants grown from tips. (a) Streak. (b) Healthy.

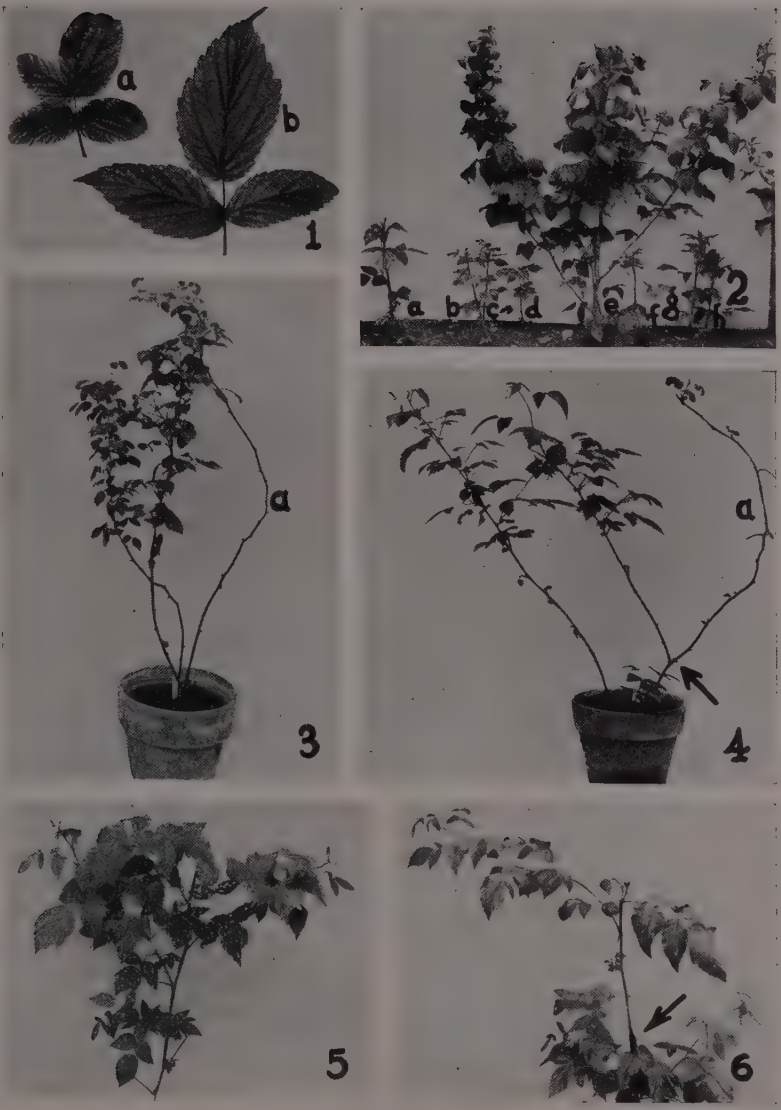

PLATE VII

Fig. 1. Curl (a) and healthy (b) leaves of Cuthbert red raspberry produced on the same cane, and less than three inches apart, but separated by a girdle.

Fig. 2. This plant was inoculated in June, 1924, at the tip of the cane shown at the left. The new shoots shown were produced in August. All were attached to the same root system: *a*, *d*, *g*, and *h* were healthy and *b*, *c*, *e*, and *f* showed decided curl symptoms.

Fig. 3. Plant having one cane (a) inoculated by curl, August 1, 1925. The plant was photographed February 24, 1926, at which time all parts showed curl symptoms.

Fig. 4. Plant inoculated on the same date as the plant in Fig. 3. The inoculated cane (a) was girdled at the time of inoculation at the point indicated by the arrow. The photograph was taken February 24, 1926, at which time curl symptoms were confined to the inoculated cane. The curl cane died in March and the rest of the plant remained healthy through the season of 1926.

Fig. 5. A cane from a Cuthbert red raspberry hill having four canes, one of which was infected by curl. The cane shown was cut back to a heighth of two feet. All laterals produced showed curl.

Fig. 6. A cane from the same plant as that shown in Fig. 5. This cane was cut back and girdled. Curl symptoms showed on laterals below the girdle while those above appeared healthy.

PLATE VIII

Fig. 1. Results of a girdling experiment. This plant had cane (f) inoculated by curl, June 12, 1925. The girdling was done July 22nd and the plant was photographed September 5th. Cane (a), complete girdle, healthy shoot above girdle, curl shoots below. Cane (b) partial girdle, curl shoots both above and below the injury. Cane (c) came through the soil after the inoculation was made and shows curl. Cane (d) partial girdle, all shoots diseased. Cane (e) complete girdle, healthy shoot above and curl shoots below girdle. Cane (f) inoculated. Cane (g) cut off even with the surface of the soil, but produced no shoots. Cane (h) uninjured and remained healthy. (Inset) Girdles and partial girdles of cane *a*, *b*, *d*, and *e*, as they appeared at the conclusions of the experiment.

Figs. 2 and 3. Plants (a) and (b) of Fig. 1.

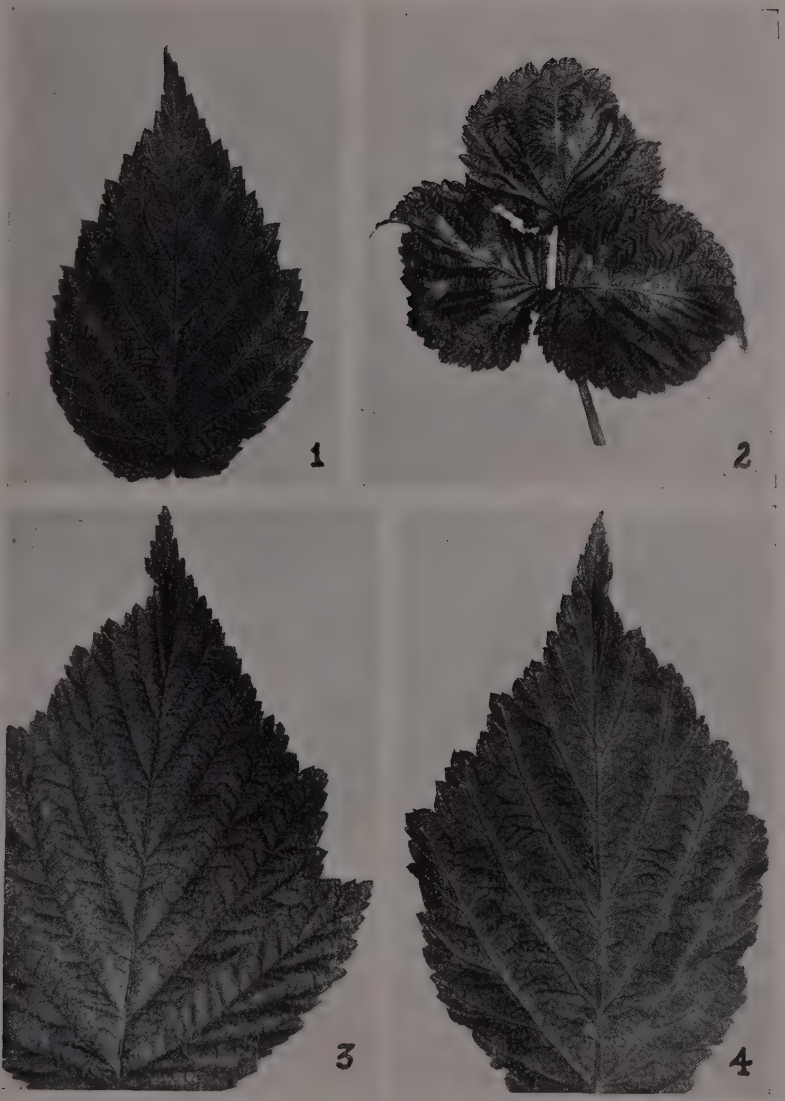

PLATE IX

Fig. 1. Frost injury on Cuthbert raspberry leaflet. Three-fourths natural size.
Fig. 2. Mildew on leaf of Cardinal raspberry. Three-fourths natural size.
Fig. 3. Red spider injury on leaflet of the June variety. Natural size.
Fig. 4. Frost injury on leaflet of the June variety. Natural size.

PLATE X

Fig. 1. Curling of leaves of blackberry caused by *Aphis rubi*. Natural size.
Fig. 2. A type of red spider injury on black raspberry. Natural size.

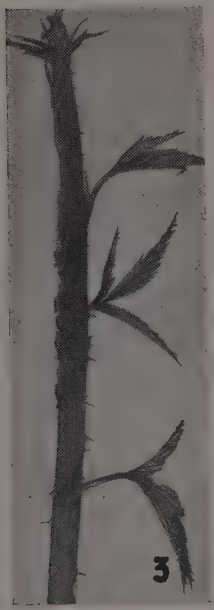

PLATE XI

Fig. 1. *Aphis rubiphila* on young fruiting laterals of red raspberry. Natural size.
Fig. 2. *Amphorophora rubi* on stem and leaves of red raspberry. Reduced.
Fig. 3. *Amphorophora sensoriata* on stem of black raspberry.
Fig. 4. *Amphorophora rubi* on leaf of red raspberry. Natural size.

hours seemed to be sufficient time for the insects to take up the virus and become effective in transmitting the disease. These aphids, in each case, were allowed to remain on the inoculated plants for several days and no information has been obtained regarding a possible incubation period for the virus in the body of the insect. Likewise no information has been obtained regarding the length of time these viruliferous aphids must feed on healthy plants before transmitting disease.

Table 4.—Results of Experiment in Which Cuthbert Plants Were Inoculated With Curl by Different Numbers of Individuals of Aphis rubiphila.

	No. of aphids per plant and results							
	1	2	4	6	8	10	50	0
Healthy plants	13	14	11	11	5	7	3	16
Diseased plants	3	2	5	5	11	9	13	0

Influence of Number of Aphids Used in Inoculation on Percentage of Infection. During the summer of 1923, experiments were performed to determine the number of individuals of *Aphis rubiphila* necessary to produce the maximum percentage of infection of inoculated plants. Table 4 shows results of one series of tests. It will be noted that one aphid per plant was sufficient to transmit curl, but only a small percentage of infection was produced in this series. Results in this experiment are not altogether consistent and other tests have given considerable variation as to the number of aphids required for maximum infection. However, numerous inoculations in which ten aphids per plant were used have given approximately the same results as have inoculations in which fifty or more insects were placed on each plant.

Longevity of Curl Virus in the Body of the Aphid. Evidence bearing on this point was obtained in the spring of 1924 and again in 1925. Large colonies of aphids, of the species, *Aphis rubiphila*, which had developed on Cuthbert plants affected by curl were removed from these plants and placed on moist filter paper in deep culture dishes. These aphids were used to inoculate healthy Cuthbert plants. Ten aphids were placed on each plant and ten plants were inoculated in each test. In the experiments of 1925, aphids were removed after different time intervals varying from one hour to forty-eight hours as shown in Table 5. All inoculations except the twenty-four hour and the forty-eight hour tests were made with wingless aphids. However, after eighteen hours, winged forms began to appear and the twenty-four and the forty-eight hour tests were made with winged individuals. Few aphids remained alive after the forty-eight hour inoculation so that it was not feasable to make tests using longer time intervals. Disease resulted in each of these tests in the percentages shown in Table 5. The twenty-four and forty-eight hour inoculations have been repeated several times. Infection has resulted in each of these trials.

After it was found that forty-eight hours was approaching the limit of time these aphids could be kept without food, attempts were made

Table 5.—Curl Infection Results in Experiment in Which Viruliferous Individuals of Aphis rubiphila were kept in Deep Culture Dishes for Varying Time Periods Before Being Used for Inoculation.

	Results after aphids had been removed from diseased plants for stated number of hours before inoculation												
	Check	Direct transfer	1 hr.	2 hrs.	3 hrs.	4 hrs.	5 hrs.	6 hrs.	7 hrs.	8 hrs.	12 hrs.	24 hrs.	48 hrs.
Diseased plants	0	6	3	2	3	1	4	4	2	5	2	4	6
Healthy plants	10	4	7	8	7	9	6	6	8	5	8	6	4

to determine by other means how much longer the virus present in the aphids' body remained active. Viruliferous aphids were transferred to plants of the apparently curl-immune St. Regis variety and numbers removed daily for five days and placed on healthy plants, sixteen plants being inoculated each day. Infection was obtained in each lot, the numbers becoming infected being respectively, 14, 8, 11, 8, 10. A second test was made by keeping viruliferous aphids on Perfection, another variety apparently immune to curl. These Perfection plants, however, had red raspberry mosaic. The aphids from curl plants were allowed to remain on these mosaic Perfection plants for two weeks, and then transferred to sixteen healthy Cuthbert plants. Later eleven of the Cuthbert plants developed curl but none of these plants showed symptoms of mosaic. Virus-free aphids of the same species as above were allowed to feed on the Perfection plants from which the curl aphids had been removed. After two days these aphids were transferred to healthy Cuthbert plants. These plants, however, remained healthy.

It seems probable from the above experiments that curl virus remains active in the body of *Aphis rubiphila* for a considerable time, and possibly may persist so long as the insect lives. However, Smith (28) has shown that the virus is probably not carried from one generation of this aphid to the next and that each insect must feed on a diseased plant before becoming a carrier.

Temperature Relations of Virus Diseases. Field Observations

With the exception of curl and possibly streak, virus diseases of raspberry show striking responses in the development of symptoms to changes in temperature. Curl, however, on both red and black varieties, presents the same type of curled and darker green leaves and the same relative amount of stunting when subjected to low temperatures as it does when affected plants are grown at higher temperatures.

In striking contrast to curl, red raspberry mosaic symptoms are markedly influenced by temperature; low temperatures bring out symptoms which may be partially or wholly masked during warmer weather. The variety affected also seems to exert considerable influence on the type of symptoms produced at any particular temperature. Thus on the Cuthbert variety mottling will show on some parts of the foliage throughout the growing season, and mottling on some plants is quite distinct even during the warmer part of the summer.

On other plants, under similar conditions mottling may be of a very mild type. The length of time a plant has been affected by this disease also seems to have an influence on the degree of mottling and, of course, has a very decided influence on the size and vigor of the plant.

A Perfectoin plant may show more or less distinct leaf distortion and mottling early in the season and in the fall but during July and August mottling usually takes the form of yellow blotches and the leaves are more nearly normal in shape. The Latham shows considerable masking at ordinary summer temperatures and on the St. Regis practically no symptoms of mosaic are evident except on the very early or very late growth. Wild red raspberries (*Rubus strigosus*) in the vicinity of Lansing may carry mosaic virus through the entire summer without showing any characteristic mottling. This species over the southern half of the state is quite generally infested but except after very cool periods, it is difficult often to point out symptoms of either mottling or dwarfing. However, even in the southern part of the state, some plants of this species show distinct signs throughout the growing season. In the northern part of the state, mottling is more apparent; and Dr. E. A. Bessey has observed that, in the Upper Peninsula, leaves are distinctly mottled and often abnormal in shape even during July and August.

Red raspberry mosaic on blackcap varieties is much more severe in its effect and the influence of temperature is not so apparent. Mottling may be masked but other symptoms such as discoloration of cane tips and leaf petioles and general stunting and rosetting are so marked at all times, that diseased plants are quite conspicuous. The fact that symptoms are so apparent is probably due to the short time required for the disease to produce a stunted and necrotic condition which may persist through the remainder of the season. The first spring after infection takes place, plants produce new canes which for a time appear normal. However, after these have attained a height of eight inches or more, the tips usually cease to grow and become very brittle. It is possible that the vigor of this first flush of growth is made possible through a lack of dispersion of virus through the plant in sufficient quantity markedly to check growth. Plate III, Figure 4 shows a plant of a black variety as it appeared in September after infection the preceding season. In the foreground, the shoots which were produced in May are seen. The larger shoots, mostly in the background, grew during the last week in August and early September, a period of very high average temperature. These latter shoots, when they first started growth and until they were of considerable length, appeared normal except that the cane diameter was small. No mottling could be noted and the leaves were normal in size and shape. As cooler weather came on, a marked change in these tips took place and growth stopped. Many of the tips turned black and died back for some distance, while others developed the type of rosette shown in Plate III, Figure 1.

From the data thus far available, it would appear that the optimum and maximum temperatures for the appearance of symptoms of mild mosaic are lower than for any other virus disease of the raspberry. At certain times during the summer under Michigan conditions, practically no symptoms are evident on the foliage of diseased plants. In the field, the most satisfactory time for observing mottling is preced-

ing and during the blossoming period. The leaves of fruiting canes will often have mild forms of mottling while very little chlorosis will appear on the leaves of the first year canes. This mottling on the leaves of the fruiting canes in the absence of distinct mosaic symptoms on the leaves of the first year canes can probably be accounted for on the basis of temperature. Leaves on the fruiting canes are not only shaded to some extent but are produced very early in the season at a time when the temperature is low enough to allow for the appearance of symptoms, and such leaves retain their mottled condition until after harvest or until they begin to yellow and die. After the fruit is picked, leaves of the fruiting canes deteriorate to such an extent that distinct symptoms are not evident. Under these conditions it is sometimes very difficult to locate mosaic plants.

At the time of the formation of leaves on the fruiting canes, the first year canes are in the early stages of development and only the lower leaves, which soon become discolored and drop, are produced at the same time and under comparable conditions to those of the fruiting canes. It has been observed repeatedly that the lower leaves on the first year canes of mosaic plants are mottled. The foliage of the first year canes of mosaic plants grown in the greenhouse during February and March has uniformly developed the same characteristic mottling as that found on the fruiting canes of these same plants. This mottling is also similar to that found on leaves of fruiting canes of diseased plants growing under field conditions.

Young canes towards the end of the season will usually show mottling on the tip leaves, and rings of mottled leaves may often be found on other parts of the canes, marking periods of rather low summer temperatures.

The symptoms of yellow mosaic seem to vary less in response to ordinary summer temperature changes than do those of mild mosaic or of red raspberry mosaic. High temperatures may to some extent mask the mottling, but generally, diseased plants have the characteristic stunted growth and yellowish cast to the leaves. In rate of growth of new shoots, however, diseased plants respond to increase of temperature in much the same way as do plants of black varieties affected by red raspberry mosaic.

The development of streak apparently shows little relation to changes in temperature so far as general appearance of affected plants is concerned. However, only two season's observations are available on this disease for Michigan conditions. Wilcox (31) has described no very striking temperature relation for Ohio conditions and Rankin (24) reports no outstanding responses to temperature changes in New York state. However, Wilcox has found striping of the canes to be a rather constant character, though not an unfailing one, in Ohio plantings. In the season of 1925, little streaking was found on the main canes of plants in Michigan, but on the laterals this symptom was very common. Since the highest temperatures for the summer came during the period of growth of laterals, after the "tipping back" of new canes, and since there is apparently more streaking of canes in Ohio fields than in Michigan, it is possible that streaking is a response on the part of the plant to high temperatures.

Temperature Studies Under Controlled Conditions

During the fall of 1924, diseased plants as uniform in size and character of symptoms as could be found were selected for the purpose of making a more detailed and careful study of the influence of the temperature factor in symptom variation. The varieties used are shown in Table 6 and the diseases studied are red raspberry mosaic, curl, and mild mosaic. These plants were taken to Madison, Wisconsin, where, through the courtesy of the Department of Plant Pathology of the University of Wisconsin, they were grown at different temperatures. The plants were all started in one house and grown at the same temperature until the largest ones were about three inches high. The most uniform plants were then divided into four lots, each lot containing plants representing the disease and varieties to be studied. The plants were placed in a series of greenhouses in which the temperatures were regulated by means of thermo-regulated steam pipes and cold air fans as nearly as possible at 16, 20, 24, and 28 degrees Centigrade, respectively. The temperatures of these greenhouses varied slightly from that desired. To check upon the significance of these variations parallel experiments were conducted in Dr. J. G. Dickson's (8) constant temperature chambers which were run at 16, 20, 24, and 30 dgrees Centigrade, respectively. These checks gave substantially the same results as plants outside of the chambers, except for leaf modifications attributed to differences in light conditions.

Curl symptoms were marked and typical at all temperatures, and

Table 6.—A Summary of Results of Experiments to Determine the Relation of Temperature to Expression of Symptoms of Mild Mosaic, Red Raspberry Mosaic and Curl.

Variety	Disease	Results on plants grown at stated temperatures:				
		16 degrees C.	20 degrees C.	24 degrees C.	28 degrees C.	Number of plants
Cuthbert	Red rasberry mosaic	Mottling very distinct. Leaves distorted	Mottling distinct. Leaves normal size	Mottling marked but of mild type	Very little mottling on few leaves. Most leaves showed no symptoms	40
Cuthbert	Curl	Plants small but curl typical	Typical curl	Typical curl	Typical curl	20
Cuthbert	Curl + Mosaic.	Mottling distinct Leaves distorted deeper green than normal	Mottling mild Leaves slightly curled, deeper green than normal	Mottling mild Restricted to yellow spots. Leaves normal in size and shape	No mosaic symptoms Curl symptoms marked but leaves less curled than on curl only plant	20
Munger	Mild mosaic	Leaves distorted twisted, blistered, very abnormal	Blisters distinct but leaves show little distortion	Leaves normal in size and shape Mottling restricted to yellow spots	No symptoms of mosaic Leaves normal in appearance	20
Columbian	Red raspberry mosaic	Leaves much twisted and otherwise distorted. Mottling very pronounced	Leaves and plants nearly normal in shape and size. Distinct elevated green areas	Leaves and plants normal in size and shape, mottling restricted to yellow spots	Leaves and plants normal no mottling	20
Cuthbert	Healthy	Normal	Normal	Normal	Normal	20
Columbian	Healthy	Normal	Normal	Normal	Normal	12

the only difference to be observed in plants at the different temperatures was in size attained, the largest plants being produced at the highest temperature.

Symptoms of red raspberry mosaic were quite distinct at 16 degrees and the disease also caused considerable leaf distortion and dwarfing at this temperature on both the Cuthbert and Columbian varieties. As the temperature was increased, symptoms became less marked and at 28 degrees the Columbian plants showed no signs of mosaic. The Cuthbert variety also produced normal foliage except for two or three leaves on each plant which showed a suggestion of mottling.

Perhaps the most interesting results from this series of tests are those obtained with Cuthbert plants having both curl and red raspberry mosaic. At 16 degrees, mosaic symptoms on these plants were very distinct and except for the deeper green color and the slight curling of the leaves the plants were very much like those affected by the mosaic virus alone. The presence of mosaic virus in curl plants seemed to cause less curling of the leaves, an observation which has also been made under other conditions. At 20 degrees, mottling remained quite distinct but at 24 degrees mosaic symptoms were very mild, consisting mainly of faded spots in the leaves. At 28 degrees, all signs of mottling were masked, but the tendency for a decrease in the amount of curling of the leaves was still noticeable.

Mild mosaic reacted very much like red raspberry mosaic. There was less mottling at 24 degrees, however, perhaps indicating the temperature maximum for this symptom is slightly lower than for red raspberry mosaic, probably being very little above 24 degrees. The masking temperature for red raspberry mosaic is probably very close to 28 degrees and curl will probably be quite characteristic at any temperature which will permit growth of the affected plant.

On the Movement of Curl Virus in Plants

In July 1923, it was noted that, in a small patch of selected Cuthbert stock growing on the Horticultural grounds, twenty-three separate infections were beginning to become evident. Previously there had been no curl in this planting. To determine whether the curl virus had moved down to the root system, the twenty-three canes were cut off even with the ground and removed from the patch soon after infection became apparent. In all cases the new shoots which grew from the severed canes were diseased. It was found, however, that all of the canes in each hill, which were above the ground at the time infection probably took place, remained healthy throughout the season.

It was also observed that many of the shoots which grew from the root system after the infected canes were removed showed curl. A count of these small shoots from the twenty-three plants showed that approximately forty per cent showed the symptoms of curl while about sixty per cent were apparently healthy. Figure 2 of Plate VIII shows a similar plant in which the infected canes was not removed. Four curl and four apparently healthy young shoots can be seen. All of the young shoots were later dug and found to have a root connection with the parent plant.

Observations have been continued each season since 1923 and it has been found that, when one cane in a hill of six or eight is infected with

curl, the canes not infected but above the surface of the soil at the time of the inoculation remain healthy during the growing season, while shoots which grow from the root system after the initial infection frequently show curl. Older canes usually continue growth through the season and the growing tips of all canes, regardless of size, should be physiologically and anatomically similar, so that in all canes growth conditions would seem to be favorable for the appearance of curl if the virus were present.

Additional evidence has been obtained on the movement of curl virus in plants by means of girdling experiments. A number of investigators have for several years believed that the chief reservoir of virus in a mosaic plant is the phloem. The woody nature of the raspberry plant has afforded an opportunity for girdling experiments which may throw some light on this point.

In 1924, fifteen two year old Cuthbert plants, growing in boxes, were selected and on July 3 were pruned back so that each plant had from four to six full sized canes. In each box one cane was girdled about three inches from the ground, caged and inoculated above the girdle. Six of the inoculated shoots showed decidedly curled leaves after forty days and continued to show distinct curl symptoms until the leaves were killed by frost at the end of the season.

Aphids were transferred from three of these curled canes to healthy Cuthbert plants. The development of curl on this lot of plants showed that the virus of curl was present in the part of the girdled cane above the girdled area. All new shoots produced from the original inoculated plants during the season of 1924 remained healthy and all of these plants have remained healthy through the season of 1925. As a check on this experiment one cane of each of these plants was inoculated, but not girdled. These three plants were infected and new shoots growing from the sides of the boxes showed curl eight weeks after the inoculations were made. During 1925 all parts of these plants, including both fruiting and first year canes, showed curl.

This experiment has been repeated a number of times and several variations have been introduced, in which some canes were only half girdled, others had only a very small strip of bark remaining, and still others were completely girdled. In each infected plant in which any tract of phloem was left to bridge the girdle, the virus has passed down into the root system and the entire plant has eventually become affected. In every case of complete girdling, the plant parts other than the cane inoculated have remained healthy.

Figure 4 of Plate VIII shows a small plant which had two canes, one of which was girdled and inoculated in July 1925. Curl symptoms were distinct in thirty days, and remained evident until frost. The plant was protected during the winter and brought into the greenhouse in February 1926. The picture was taken in March to show the girdled curl shoot and the apparently healthy remaining part of the plant. Figure 3 of the same plate shows another plant which received the same treatment except that a small amount of bark was left to bridge the girdle. All parts show curl. These experiments seem to indicate (1) that the curl virus can be confined to the inoculated shoot for an indefinite period by a simple process of girdling, (2) that a relatively small amount of bark bridging a girdle is sufficient to permit the pas-

sage of the curl virus from the inoculated part to the parts below the girdle.

Attention was next directed to the larger canes of plants in which one cane had become infected. It was found that curl virus could be induced to enter these canes, which would otherwise remain healthy through the season, if they were cut back to a considerable extent and lateral buds stimulated to grow. It was further found that this virus could be limited to any given part of the cane by placing a girdle at the appropriate place at the time the top was cut away. Plate IX, Figure 1 shows a three-year old Cuthbert plant which was grown in a box. The long cane shown in the photograph was inoculated, and after symptoms of curl had appeared some of the shoots were partly girdled, some completely girdled and others left as checks.

Six weeks after girdling the plant was removed from the box and the soil washed from the roots. All shoots were found to have a root connection with the main crown. Canes *a* and *c* of the picture were completely girdled; curl shoots are seen below the girdle and healthy ones above. Cane *c* came through the soil after the original cane was inoculated and shows curl. Canes *b* and *d* were partly girdled; each shows curl branches both above and below the partial girdle. Cane *f* is the inoculated one. Cane *g* was cut off even with the ground but did not grow. Cane *h* received no treatment and was normal. This cane was transplanted to a pot and found to remain healthy through a second season. Canes *a* and *b* are shown again in Figures 2 and 3 of Plate IX. Eighteen plants have been given a treatment similar to the above and all have reacted in essentially the same manner. Aphids have been transferred from the apparently healthy shoots above girdles and from diseased shoots below. No infection has been obtained from apparently healthy shoots, while it has been easy to demonstrate the presence of virus in shoots below girdles.

Girdling apparently does not seriously interfere with the function of shoots above the girdle. Growth is sometimes more rapid than normal and the leaves are often somewhat pale, but otherwsie there is no great change in appearance. Curl canes have also been girdled and it is found that on secondary shoots produced above the girdles, the curl symptoms are typical. Healthy shoots above girdles have also been inoculated and show curl symptoms at the end of the average incubation period, indicating that there are no physiological disturbances due to girdling itself which would tend to suppress symptoms if the virus were present.

It has been pointed out that the larger first year canes in a hill in which one cane has become infected remain healthy during the rest of the growing season. It has been noted repeatedly, however, that these uninoculated canes are in nearly every instance curled the second season, and that all of the new canes of the second season show curl. Rarely is a healthy cane found on a plant infected the preceding season provided the root connection between such canes remains intact. This condition presents a problem of determining at what time the virus makes its appearance in these uninoculated canes. In the fall of 1924, a plant of a purple variety (Haymaker) which roots at the tips of the canes was found which had two curl canes. This plant had six other vigorous canes which were apparently healthy. These had been tipped

back, probably before infection took place, and lateral buds had grown producing nineteen shoots which were tipped in September. The following spring just after growth started, the rooted tips were severed from their connection with the mother plant and grown through the season. All remained healthy indicating that the virus had not moved to the tips of uninoculated canes during the season of infection. The canes from which the tips had been removed were next girdled about twelve inches from the ground at six day intervals, beginning when the buds were showing green. The first two canes girdled produced apparently healthy fruiting laterals above the girdles and diseased shoots below. On the last four canes girdled, all laterals both above and below the girdles showed curl. In this experiment there was great contrast between healthy and diseased parts due to the decided dwarfing effect which curl has on the Haymaker variety.

A similar girdling experiment was tried on four Cuthbert plants in which one cane of each plant had been inoculated the season before. Here again it was found possible to obtain apparently healthy shoots above the girdle providing the canes were girdled before the new fruiting laterals were two inches long. It was also noted that even those shoots coming out from below girdles and on ungirdled canes were at first normal in appearance and that the first four or six leaves produced showed distinct curling of the leaves, while the shoots on the opposite side appeared normal.

In the experiments described above, an attempt has been made to follow some of the movements of the curl virus through the diseased plants from the time of initial infection until the virus became generally distributed through the plants. The results obtained seem to suggest a possible correlation between the path of virus movement and what is commonly regarded as the most important channels of food translocation. This correlation has seemed to exist in several different types of experiments performed at different seasons of the year.

In some of the experiments in which first year canes were inoculated, plants were selected in which all of the above ground parts had been removed except from four to seven first year canes varying in height from two to four feet. One cane in each hill was inoculated. The virus passed down into the root system and into some of the suckers which were later produced by the root system. These suckers, until they grew through the surface of the soil, were drawing on some part of the rest of the plant for food. The virus in one instance traveled a distance of eleven feet from the point of inoculation to the tip of one of these young shoots.

On the same plant, however, the larger canes of approximately the same size as the inoculated one remained apparently healthy during the remainder of the growing season, and as suggested by girdling experiment the virus did not move into these canes until after growth had started the following season. The larger first year canes of these plants were at the time of the inoculation presumably manufacturing food in excess of their needs for growth and the movement of the excess food would probably be in the direction of the root system. Seemingly so long as the factor favorable for this condition obtained the larger uninoculated canes remained free from disease. However, when these uninoculated canes were pruned back to such an extent that it

might be presumed that they became for a time at least partially dependent on the remainder of the plant for organic food, the curl virus passed up into these parts and curl symptoms were noted in the new growth which was produced by these first year canes.

These results, fundamentally, may not be greatly different from those obtained in experiments in which the uninoculated canes were allowed to grow normally through the first season but which were girdled for the purpose of studying the virus movement into fruiting canes the season following infection. It has been pointed out that the virus apparently did not move up into these canes until after growth was well started. In considering the food relations in such canes, it seems entirely possible that the food reserve in the canes themselves may have been used for the earlier growth and that this may have been followed by a drain on the food stored in the root system, a reservoir built up the previous season by contributions from both diseased and healthy canes. Thus the movement of curl virus into these canes in the spring may parallel the movement of food from the root system into such canes.

This apparent correlation between food translocation and virus movement would seem to offer considerable possibilities for further investigation from a physiological as well as a pathological viewpoint. If the two phenomena are so closely parallel as now seems probable, the curl virus may serve as an excellent indicator for studies in food translocation in the raspberry plant. Further investigation may also reveal important relations between elaborated food and the virus itself which may possibly have a bearing on the nature of the causal agent. The raspberry plant offers special opportunities for studies in virus movement as well as of food translocation. Because of its woody nature it is well adapted for girdling experiments. Its methods of reproduction, its freedom from infection except by aphids, its numerous distinct virus diseases, its varietal immunity features and its perennial tendencies are other characteristics which seem to make it a very desirable plant for experimental work of this type.

Varietal Susceptibility

The varietal reactions of raspberries to virus diseases of different types afford many angles for study of disease susceptibility. In some varieties, there seems to be only a slight degree of susceptibility. Many varieties are apparently immune to some of the virus diseases, though no variety is known to be immune to all of them. Wide ranges of disease tolerance are found in raspberry varieties. The effects of red raspberry mosaic seem to be more subject to wide variation due to varietal influences than are the symptoms of any of the other virus diseases of this group of plants. Perfection plants affected by this disease live and produce fair crops of fruit for a number of years. The so-called everbearing varieties such at St. Regis and Sunbeam are apparently injured only to a very slight extent by this trouble, while Plum Farmer plants are sometimes killed in less than two years by its attacks. The degree of apparent resistance or susceptibility of some varieties seems to a considerable extent to be due to the feeding habits and movements of the insect vectors.

Aphis rubiphila, for example, seems to prefer feeding on a Cuthbert

plant to any other variety. This added to what appears to be an extreme natural susceptibility of this variety to curl is undoubtedly the explanation of the large percentage of curl found in many Cuthbert plantings. On the other hand, *Amphorophora rubi* feeds more readily on such varieties as Perfection and King and the wild red raspberry than it does on Cuthbert. This last named variety also seems to possess a natural resistance to mosaic infection, since it is extremely difficult to obtain more than ten to twenty per cent infection even when large numbers of aphids are used. The relation to feeding of *Amphorophora rubi* and the natural resistance probably account for the fact that the Cuthbert, although one of the oldest varieties, is the only red variety in the state relatively free from mosaic.

The red and hybrid varieties so far as has been determined are susceptible to only two distinct virus diseases; namely, curl and red raspberry mosaic. Hybrid varieties seem to be susceptible in most cases to the virus diseases of the red parent but immune or very resistant to those of the black parent. Mild mosaic and yellow mosaic have never been recognized on purple varieties although three hybrid forms under observation have been exposed to infection for four years. Inoculations have also failed to lead to the development of symptoms of these mosaics on purple varieties.

Among the black varieties, there does not seem to be the variation in resistance to different types of virus diseases which is present in red varieties, except in the case of curl to which Cumberland is very susceptible, Gregg is relatively susceptible and Kansas and Plum Farmer are very resistant or immune. All black varieties appear to be about equally susceptible to mild mosaic. From field observations, it might be suspected that all black varieties are also about equally susceptible to red raspberry mosaic and yellow mosaic and that considerable resistance to infection was generally characteristic. However, as a matter of fact, all commercial black varieties seem to be very susceptible to these diseases, and the small number of diseased plants found is probably due to quick death of infected individuals and dislike of aphids for such plants.

Wilcox (31) reports that the Hoosier and the Cumberland are quite susceptible to streak and that Kansas and Plum Farmer show some resistance. Not enough streak has been found in this state to draw any accurate conclusion regarding varietal susceptibility under Michigan conditions.

The varietal reactions of raspberries to virus diseases merit much more careful consideration than this subject has received. Both the practical and scientific aspects of the problem offer a wide field for further investigation. The possibilities of combination of different diseases on the same plant and the separation of these again by means of varietal immunity and aphid peculiarities would seem to be almost endless. Hybrid varieties also offer an interesting field for study.

Maladies and Injuries Which May be Confused With Virus Diseases

Mildew. Some of the red and purple varieties are especially susceptible to mildew, *Sphaerotheca humuli* (DC.) Burr. The Latham and Cardinal varieties in Michigan have shown very marked symptoms which in certain stages very closely resemble types of mosaic mottling.

Leaves have lighter colored spots, and at times mildew may cause the leaf to become considerably twisted and otherwise distorted (Pl. XI, Fig. 2.) The leaves of the Cardinal variety are often very much stunted. Pubescence is often absent in certain spots on the lower side of the leaf and at times spots appear slightly water soaked. Usually the mildew fungus can be seen on the basal side of the leaf, but sometimes spots appear which are similar to the ones described above, but on which no superficial growth of mycelium or spores can readily be found. Such spots, especially on the Latham and King are sometimes difficult to distinguish from red raspberry mosaic.

Aphid Injury. The blackberry aphid, *Aphis rubi*, causes a very striking and marked curling of the leaves of blackberry plants which in some cases is almost an exact duplicate of symptoms caused by curl. These aphids feed mainly on the young leaves near the tip of the canes giving these the appearance of a cane recently infected.

Quite characteristic curling on Cuthbert also has been produced in cages in which large numbers of *Amphorophora rubi* were kept (Pl. XII, Fig. 2). In these cases, curling of the leaves was characteristic enough to be mistaken for beginning curl symptoms, but the plants produced normal leaves soon after the aphids were removed.

Leaf Hopper Injury. At certain times during the summer when leaf hoppers are abundant, the leaves of red varieties at the tips of the canes may begin to roll and look very much as if they were showing first signs of curl. Nearly every cane in a planting may at times show this trouble and even the older leaves may be affected. Leaf hoppers feed on the main veins and these veins on the dorsal side soon take on a distinct brownish discoloration. Usually this characteristic is sufficient to determine the true nature of the trouble.

Frost Injury. For some years, a peculiar type of marking has been observed along the veins of leaves of many varieties of raspberries. This injury is shown in Plate X, Figures 1 and 4, and consists of a row of chlorotic spots on each side of the larger veins. The spots are about as wide as a pencil mark and from one to two millimeters long. A more severe form of injury causes the leaflets to become more nearly lanceolate, and the tissue between the veins is thrown into elevations and depressions. Such leaves may take on a slightly greener color and in such cases a semblance of mottling is produced.

Leaves showing these various types of injuries appear in the spring and consequently are usually to be found near the base of the fruiting shoots and on the lower parts of the new canes. Leaves once injured, however, retain the characteristic markings well through July. The appearance of these conditions has been associated with late frosts in the spring. The injury has never appeared in the greenhouse nor on plants otherwise protected. In the spring of 1925, potted plants in the open showed considerable stippling along the veins soon after a heavy frost, while plants of the same lot and of the same size and age, which had a few days before been placed in cheesecloth cages, showed no sign of injury. During the spring of 1926 many more tests were made by placing plants outside of the greenhouse on nights when frost was predicted. It was found that all of the various stages of injury noted under field conditions could be reproduced in this way, while check

plants not exposed to frost remained normal. After exposure to low temperatures, a six to ten day period was required before evidence of injury appeared. Only about two leaves from each bud were injured by any one frost. The injured leaflets at the time they were subjected to low temperatues were only from a quarter to three-quarters of an inch long. The smaller leaves as well as the larger ones seemed to suffer no ill effects except in cases where the older leaves were partially killed by freezing.

Red Spider Injury. Raspberries are at times damaged to a considerable extent by red spider and, even during years of mild infestation, the spiders are sufficiently abundant to cause numerous abnormal markings on leaves. The typical injury is a small circular light colored spot. The location on the leaf of this spotting varies considerably. Sometimes much of the spotting is midway between veins but often, especially on black raspberries, the spots occur in greatest numbers in rows on each side of the main veins Plate XI, Figure 2. Under these conditions, the injury may to a considerable extent resemble mild frost markings, though such spots are usually less uniform in spacing and more inclined to be circular than are frost markings. Red spider injury in general will not be confused with well advanced mosaic mottling but there is a possibility of confusing this injury with frost damage and with very early stages of mosaic. Later in the season injury due to red spider may become so prevalent that symptoms of true mosaic mottling may be rendered obscure.

Spray Injury. Standard sprays of almost any kind are likely under certain conditions to cause injury to raspberry foliage. A common type of injury is burning of the leaves around the edges and in spots throughout. In addition to this burning there are apparently injuries in which the tissue is not killed, but the leaves merely have a certain amount of the chlorophyll destroyed. This condition has been found in fields sprayed with lime-sulphur and in fields in which Bordeaux mixture has been applied. Spray drops on the top side of the leaf do not often seem to produce a chlorotic condition but those which stick to the lower side seem to have at times a bleaching effect and immediately above such spots the leaf tissue takes on a lighter color which in some cases is almost indistinguishable from certain forms of mosaic mottling.

Control

There are two aspects which call for attention when the problem of control of raspberry virus diseases is considered. The first has to do with the control measures used and degree of control desired by individual growers with production of fruit as a primary consideration. The second aspect has to do with the production and maintenance of stocks of virus-free plants of the best commercial varieties with the end in view of saving these varieties from "running out." If growers were able to secure virus-free stock for their young plantings, it it doubtful if virus diseases in many instances would be of any great economic consideration in commercial fields so far as fruit production alone is concerned. It seems probable that the spread of virus diseases of bramble fruits is much too slow often to cause serious loss during the life of a single planting provided the stock is clean at the beginning.

The key to the control situation then lies in establishing sources of disease-free stock and continuing these sources in spite of the frequent introduction of virus diseases from the wild species of Rubus which are prevalent in waste places over the greater part of the United States.

Resistant Varieties. The solution of problems of plant disease is being sought more and more in the field of breeding for resistant varieties. The most desirable variety of raspberry which could be produced from the standpoint of virus disease control—short of complete immunity—would be a kind as resistant as possible to infection but very susceptible to injury after infection. An immune variety no doubt is a possibility, though no variety of any commercial value immune to all the virus diseases is known. However, the Cardinal because of its apparent resistance or immunity would seem to be a valuable parent with which to start work looking towards results of this kind. If immunity is not obtained, then enough susceptibility to ravages of disease to make it easy to detect infected plants quickly will be a considerable aid in keeping new varieties which are distributed by plant breeders relatively free from virus troubles. Those varieties which show least symptoms are ones which will offer most difficulty in keeping stocks of relatively disease-free plants. A variety of raspberry which could be propagated from seed, since virus is probably not carried in the raspberry seed, would probably be little injured by virus diseases. However, immune and resistant varieties are largely problems of the future, and the immediate need is of virus-free plants of the commercial varieties already distributed and widely grown.

Roguing Diseased Fields. In Michigan, at the present time, there are many plants of the Cuthbert, King, Gregg, Plum Farmer, and Cumberland varieties comparatively free from virus diseases. In many of these fields, it is entirely feasible for the owner, after becoming somewhat acquainted with symptoms of virus diseases, to dig out and destroy all streak, mosaic, or leaf curl plants, and secure stock which will be practically or completely free from these diseases. Red varieties are much more difficult to rogue successfully than are black or purple varieties, because of the difficulty of determining all shoots belonging to one plant and the tendency of red varieties to produce new shoots from pieces of roots left in the ground.

Plantings which have much more than ten per cent of the plants diseased will probably not in many cases pay to rogue. Such patches, so far as the grower is concerned, might better be kept so long as they pay a profit, then destroyed and a new start made with virus-free stock. Young plantings having less than ten per cent of the hills affected, however, can usually be rogued successfully. In roguing, it is important that diseased plants not only be dug or pulled out of the ground but that they also be carried out of the path and either be burned or piled at a distance from raspberries before they wilt. If aphid infested plants are left to wilt and dry in the field, *Amphorophora rubi* soon crawls from the wilted leaves and stems to the nearest feeding place, and *Aphis rubiphila* soon produces wings and flies to other plants. Thus roguing, if the diseased plants are left to wither in the

patch, may at times, depending on the number of aphids present, spread more disease than the practice eliminates.

The time in the life of a planting at which roguing is most effective is the first year. If the plants are examined the latter part of June, usually symptoms of all virus diseases can be seen if the inspection is carefully made. Aphids have usually not become numerous in such young fields and the plants are small enough to be removed from the field without much added effort. A second inspection should be made in September. Fields of this type which are carefully rogued the first season can in nearly all instances be kept clean by the removal of a very small number of diseased plants in succeeding years, provided the planting is fairly well isolated from other sources of infection. Older fields having a considerable number of infected plants require more time and effort in roguing, and results are more likely to be disappointing.

It is especially important that one who is roguing a planting have a knowledge of all virus diseases of raspberry. Red raspberry mosaic and yellow mosaic in blacks and curl in both reds and blacks are easily recognized. Where roguing is practiced these diseases are usually satisfactorily controlled. However, red raspberry mosaic in red and purple varieties and mild mosaic and streak in black varieties are more difficult to recognize. Considerable experience with these diseases is usually required before accuracy in diagnosing is attained. These latter diseases, so far as potential damage is concerned, are by far the more important. The difficulties involved in recognizing symptoms of these troubles add materially to the cost of their control by the roguing method. A few growers in the state have been very successful in practically eliminating mild mosaic and red raspberry mosaic from their younger fields of raspberries. Many others have met with disappointing results, largely it is believed because of failure to recognize and remove plants in the earlier stages of disease.

State Inspection of Nursery Stock. Regulation and inspection of nursery stock by a competent inspection service, together with the awakening of growers to the need of producing virus-free plants, seems to offer the quickest and most economical solution of controlling the virus diseases of raspberries. The Michigan nurseries buy practically all of their raspberry plants from growers. Consequently in past years nursery stock has been representative of the virus disease situation over the state. The Michigan State Department of Agriculture has adopted a policy of requiring inspection of all fields from which plants are to be sold to nurseries, each planting to be inspected at least twice during the season. Fields containing a considerable amount of disease are rejected and those containing a small amount are rogued by the inspector. Other states have adopted a similar practice. If virus diseases spread no faster than our evidence indicates, this system of inspection, with reasonable co-operation on the part of growers and nurserymen, and if efficiently done, should give satisfactory results with most of the commercial varieties grown in Michigan. The black varieties, it is believed, will give best results in spite of the greater number of diseases to which they are subject. Virus diseases in the King variety will be relatively more difficult to eliminate, and it is probable that there is little hope of ever roguing out even the major-

ity of mosaic plants in such varieties as the St. Regis by any system of nursery stock inspection.

Summary

There are apparently at least five distinct virus diseases of raspberry. The names curl, red raspberry mosaic, mild mosaic, yellow mosaic, and streak have been used to designate these troubles.

With the exception of streak, all of these diseases have been transmitted by means of aphids. Two species of aphids, *Amphorophora rubi* and *Aphis rubiphila,* have been used as agent for transmission of virus diseases. Inoculation experiments indicate that *Amphorophora rubi* is chiefly responsible for spread of the mosaics and that *Aphis rubiphila* is the most important disseminating agent of curl.

Plants have shown symptoms of curl after inoculation by a single aphid of the species, *Aphis rubiphila.* However, the percentage of infection in tests in which only one aphid was placed on each plant has been much lower than in tests in which larger numbers of aphids were used.

In tests in which viruliferous specimens of *Aphis rubiphila* were kept in deep culture dishes, these insects transmitted curl after being away from contact with living plants for forty-eight hours. There is also considerable evidence that individuals of this species which fed on curl immune hosts carried the curl virus for a period of more than three weeks.

No evidence has been obtained to indicate the presence of the curl virus in the egg stage of *Aphis rubiphila.* Plants inoculated with aphids hatched from eggs laid by aphids colonized on curl plants have in all cases remained healthy.

Temperature has a very decided influence in masking symptoms of mild mosaic and red raspberry mosaic. In temperature experiments, plants affected by mild mosaic showed no symptoms of mottling at 28 degrees C. and at the same temperature only very obscure symptoms appeared on plants having red raspberry mosaic. Under field conditions in Michigan, symptoms of yellow mosaic are distinct throughout the summer. This seems to be due in part at least to a relatively higher temperature maximum for expression of symptoms. Curl symptoms are marked at all temperatures at which affected plants will grow.

The symptoms of red raspberry mosaic vary widely with different varieties. Inconspicuous mottling is characteristic of very disease tolerant varieties such as Sunbeam; while severe mottling, necrosis, and stunting are characteristic symptoms on black cap varieties.

Girdling experiments in which the curl virus has failed to pass the girdled part indicate that the virus moves in some part of the bark. The sieve tubes would seem to be the most natural channels for such movement.

The movement of curl virus through a plant after infection is relatively slow. Some of the canes of diseased plants usually remain healthy until the spring following infection. The movement of the curl virus seems to show evidence of a correlation with food translocation.

Wide varietal ranges of susceptibility, apparent immunity, and disease

tolerance, in relation to the different virus diseases, are to be found in the raspberry group.

The most satisfactory control measures for virus diseases available for general use are: (1) careful and efficient roguing and (2) selection and production of virus free nursery stock.

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